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Epibiont relationships on hyolithids demonstrated by Ordovician trepostomes (Bryozoa) and Devonian tabulates (Anthozoa)

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Abstract. In Lower Paleozoic marine invertebrate communities of tabulate corals and trepostome bryozoans have been recognized as preferential epibionts on hyolithids. In the cases studied herein the data clearly indicates that epibionts prefer hyolithids to any other host. Several aspects of epibionts living on hyolithids are apparent: current-oriented hyoliths provide a desirable substrate and ease of feeding for them. That epibionts settle on the earliest juvenile portion of the hyolithid suggests that site selection is controlled by both composition of the juvenile periostracum and the position of the posterior dorsal conch. This is suggestive of a mutualistic relationship and possible co-evolution. The hyolithid keeps the epibiont in an optimum position for food, oxygen, and waste removal by facing into the current. The colonies on the dorsal and lateral sides of the conch provide added protection and additional mass for stability. This can be especially important in higher current regimes (hence more food, oxygen, and more efficient waste removal) or where the animal lives in habitats subject to disorienting currents.

Key words: Ordovician, Devonian, epibionts, Hyolithida, Tabulata, Bryozoa, obligate and facultative symbiosis, mutualism

Introduction

This paper demonstrates the recruitment by conchs of living hyolithids to preferentially attract different organisms (Tabulata and Bryozoa) in the Ordovician and Devonian. The growth patterns of these epibionts, which belong to several different phyla, are remarkably similar.

Paleontologists have long recognized epibionts on fossils (we use the term "epibiont" for organisms attached to surfaces of living hosts, e.g. Wahl 1989), and have observed that there is a great deal of site selectivity among epibiont organisms. There is commonly a preferred host organism and preferred area on the host for settling. In this paper we examine two taxonomically recognizable groups, tabulate corals and trepostome bryozoans, of Lower Paleozoic (Ordovician and Devonian); epibionts that preferentially settled on and recruited hyolithids. The term recruitment refers to the activity of individuals that survived post-settlement mortality on a host and are potential members of the community (Keough and Downes 1982, Osman and Whitlatch 1995).

The probability that hyolithids were vagile organisms and oriented into the current was first suggested by Duncan (1957) because of the aligned epibiotic bryozoans she observed growing on conchs. Marek and Galle (1976) described the epibiotic tabulate *Hyostragulum* situated on the dorsal surface of the hyolith *Pterygotheca* from the Bohemian and Moravian Devonian. They deduced that the epibiont grew anteriorly on the dorsal face of the conch with the oral end of the hyolithid facing into the current. They also noted that epibionts do not recruit orthothecid hyoliths. Marek et al. (1997) summarized the functional morphology of hyoliths, as well as the history of the study of epibionts on them. In this study scale models were tested in a flume and it was observed that the most stable orientation for hyolithids was facing the aperture into the current and positioning the helens to be outrigger stabilizers. They also verified the earlier findings of Marek and Galle (1976), that hyolithids were rheophilic, vagile, benthic organisms.

Specimens of *Hyostragulum* were described by Morzadec and Plusquellec (1977) from the Devonian of the Armorican Massif, and by Galle et al. (1994) from the Lower Devonian of Morocco (including an assessment of the degree of hyolith infestation by epibionts). Other hyostragulids were described by Boumendjel et al. (1997a, b), Perdigão (1972–73), and Plusquellec and Jahnke (1999), who also noted that Kayser (1889) described what seems to be a hyostragulid. Galle and Plusquellec (2002) established the family Hyostragulidae and listed its included genera. In all listed cases *Hyostragulum* is always an obligate symbiont found exclusively in association with hyolithids.

Material and methods

To test for site selectivity we examined 16,000 invertebrate specimens from a Lower Devonian (Pragian) shallow water community of carbonate mud mounds in the Dvorce-Prokop Limestone. The sample was collected in the early twentieth century from the St. Prokop Quarry in the southwest part of Prague by the well known Czech collector F. Hanuš. His are the only known large-scale collections of this formation that contain hyolithid epibionts. They are deposited in the Institute of Geology and Paleontology, Charles University, Prague. Unfortunately, the locality is no longer accessible.

The specimens were washed out from weathered parts of the section. Their number and diversity give us a good approximation of the character of the bottom community, as well as a clear picture of the organisms that epibionts preferentially recruit. The first statistical study concerning epibionts on hyoliths and other host organisms from the St. Prokop Quarry was published by Galle and Prokop (2000), in which parts of other faunas where epibionts have used hyolithids as their substrate are also briefly mentioned.

Table 1. Rows show potential hosts, columns give numbers of actual epibionts

Host/Epibiont	Specimens observed	Indet.	Rugosa	Tabulata	Bryozoa	Echinodermata	N epibionts
Rugosa	18	0	0	0	0	0	0
Tabulata	5	0	0	0	0	0	0
Brachiopoda	412	0	0	0	0	0	0
Pelecypoda	118	0	0	0	0	0	0
Gastropoda	1637	1	0	0	0	0	1
Cephalopoda	40	0	0	1	0	0	1
Hyolitha	509	0	0	132	0	0	132
Echinodermata	13557	27	1	6	1	22	57
Trilobita	42	0	0	0	0	0	0
Σ	16338	28	1	139	1	22	191

Results

Coral epibionts on hyolithid and non-hyolithid fauna in St. Prokop Quarry

In the St. Prokop Quarry, epibionts are found residing on four distinct taxonomic groups: Hyolitha, Echinodermata, Gastropoda, and Cephalopoda. Most of the Hanuš collection was examined specifically for epibionts. Unfortunately, previous researchers had removed most of the trilobites. The group with the most common epibionts are hyolithids. Here 132 epibionts belonging to the single species, *Hyostragulum mobile* Marek and Galle, 1976 (Plate I, figs 1–4) reside on a single hyolithid species, *Pterygotheca barrandei* Novák, 1891 (386 specimens) (Plate I, figs 5–8), and demonstrate a 34% epifaunal infestation. This selectivity appears to be variable. For example, in the Emsian Suchomasty Limestone near Koněprusy, the epibiont *Hyostragulum annae* Galle and Plusquellec, 2002 occurs on two hyolith hosts, *Ottomarites discors* (Barrande, 1867) (Plate I, figs 9, 10) and ?*Pterygotheca barrandei* Novák, 1891 (Plate I, fig. 11).

Epibionts are also found on echinoderms from the St. Prokop Quarry: out of 13,557 crinoid pluricolumnals, 57 epibionts (0.4%) of various taxa are found. The epibionts observed growing on crinoids are encrustations of worm-like tubes, tabulates, rare rugosans, rare bryozoans, and unrecognizable objects, but most were crinoid holdfasts. This count does not include 'myzostomid worm' structures, as they are considered to be endobionts.

The Hanuš collections, together with other smaller additional collections from the same locality, yielded the following data:

Coelenterata

Coelenterates from the St. Prokop Quarry are represented by rare small solitary rugosans (18 specimens) and favositid tabulates, other than *Hyostragulum* (4 specimens). No epibionts were observed on them.

Brachiopoda

None of the 412 brachiopods collected from the St. Prokop Quarry (Table 2) had visible epibionts.

Table 2. St. Prokop Quarry – brachiopods identified by V. Havlíček (1999, pers. comm.)

Species	Specimens	Epibionts
Cingulodermis cinctus	178	0
Clorinda sp.	4	0
Dalejina hanusi	48	0
Gypidulina tetinensis	11	0
Inarticulata indet.	2	0
Pentameracea	1	0
Plectodonta (Dalejodiscus) subcomitans	5	0
Rugoleptaena zinkeni	15	0
Spiriferidae	20	0
New genus [#1]	94	0
Brachiopoda indet.	34	0
Σ	412	0

Articulate brachiopods are suspension feeders capable of adjusting their position relative to their external environment (Richardson 1997). Many living articulate brachiopods position their pedicle to maintain essentially stable shell position over the water-substrate interface, which is essential for suspension feeders. Recent articulate brachiopods can actively inhibit an overgrowth of colonial sponges and ascidians by opening and closing their shells (Alexander and Scharpf 1990, p. 199, Richardson 1997, p. 449).

Pelecypoda and Rostroconcha

Pelecypoda and Rostroconcha from the St. Prokop Quarry (Table 3) are predominately semi-infaunal species that are

Table 3. Pelecypoda and Rostroconcha from the St. Prokop Quarry (J. Kříž, pers. comm. 1999)

Species	Specimens	Epibionts
Pelecypoda indet.	14	0
'*Conocardium*' sp.	65	0
Cypricardinia sp.	1	0
Lunulacardium sp.	3	0
Protobranchiidae	8	0
Pterineidae	27	0
Σ	118	0

indicative of a soft-bottom community. The pterineids are epibyssate and are attached to shell fragments. Rostroconchs belonging to the genus '*Conocardium*' were infaunal or deeply reclining into the substrate (J. Kříž, pers. comm. 1999). It is notable that the bivalves and the posterior ends of the rostroconchs that were exposed to a full range of near bottom currents are devoid of epibionts. Epibionts of Carboniferous rostroconchs have been described recently in Hoare et al. (2002).

Gastropoda

Gastropods from St. Prokop Quarry in the Hanuš collection and additional specimens from the National Museum collection were studied and are listed in Table 4. The National Museum collection is extensive and yielded a sample size close to the community proportions in the Hanuš collection. Gastropods in this material bear neither epibionts resembling *Hyostragulum* nor any other organism. The only potential epibiont observed is a tube-like object on a single specimen of *Neocyrtolites* sp. that might not be organic.

Table 4. Gastropods from the St. Prokop Quarry (R. Horný, pers. comm. 1999)

Species	Specimens	Epibionts
Asinomphalus ruzickai	2	0
Asinomphalus sp.	4	0
Australonema sp.	9	0
Coelocyclus rarissimus	3	0
Coelocyclus sp.	25	0
Cymbularia? sp.	9	0
Diplozone redux	78	0
Diplozone redux?	1	0
Diplozone sp.	85	0
Euconospira sp.	12	0
Euomphalidae	5	0
Gastropoda indet.	969	0
Gastropoda gen. nov.	11	0
Kodymites nestor	3	0
Liospira sp.	2	0
Loxonema sp.	9	0
Loxonematidae?	3	0
Murchisonia sp.	2	0
Neocyrtolites advena	28	0
Neocyrtolites sp.	20	1
Oriostoma sp.	34	0
Petrochus praecedens	1	0
Petrochus cf. *praecedens*	2	0
Pleurotomarioidea	96	0
'Pleurotomarioidea'	82	0
Pragoloron sp.	58	0
Rotellomphalus sp.	52	0
Sinuitina sp.	5	0
'*Subulites*' sp.	17	0
'*Subulites*' sp. + *Naticopsis* sp.	4	0
Threavia nuda	4	0
Tubomphalus sp.	1	0
Tubomphalus? sp.	1	0
Σ	1637	1

Gastropods are perceived as poor hosts for epibionts because ontological rotation produces continuous change in the orientation of the epibiont's substrate.

Trilobita

Because most of the trilobite specimens were removed from the Hanuš collection and deposited elsewhere, our results are statistically skewed. However, trilobites make up a relatively small percentage of the community population. A small sample of St. Prokop trilobites is listed in Table 5. They were identified by J. Vaněk (pers. comm. 1999) and they show no evidence of epibionts.

Table 5. Trilobites from the St. Prokop Quarry (J. Vaněk, pers. comm. 1999)

Species	Hosts	Epibionts
Crotalocephalina (C.) globifrons	1	0
Metascutellum pustulatum pustulatum	9	0
Platyscutellum rohoni	3	0
Platyscutellum sp.	1	0
Phacops (*Prokops*) *prokopi*	4	0
Reedops cephalotes	1	0
Reedops cf. *cephalotes*	4	0
Reedops sp.	1	0
Trilobita indet.	18	0
Σ	42	0

Hyostragulum on a cephalopod

Epibionts on cephalopods are uncommon and have been noted in the literature, such as in Prokop and Turek (1983; Silurian, crinoids on an orthoconic nautilid), Baird et al. (1989; Paleozoic, problematicum *Reptaria* and the bryozoan *Spatiopora* oriented along the long axis of a cephalopod), and Gabbott (1999; Ordovician brachiopods and cornulitids on orthoconic cephalopods). A single specimen of *Hyostragulum mobile* Marek and Galle, 1976 growing on a phragmocone fragment of *Thalesoceras amaltheum* Manda, 2001 (Plate I, fig. 12) was mentioned and figured in Marek and Galle (1976, Fig. 7F) as *H. mobile* growing on '*Cycloceras*' sp. *Thalesoceras amaltheum* is in fact an annulated necto-benthic orthocerid with a slightly curved conch that is commonly associated with mud-mounds (Manda 2001). The *Hyostragulum* specimen from the St. Prokop Quarry grew around the phragmocone, but is best developed on its ventral side; it could, but did not necessarily grow on the living specimen (Š. Manda, pers. comm. 2002). The orientation of *Hyostragulum* along the cephalopod conch axis is distinct: the elongation of corallites and particularly the direction of the median septa within the corallites preferentially align in the direction of the conch's aperture axis. Similar orientation of epibionts on orthoconic cephalopods has been described by Baird et al. (1989). Neither corallite morphology nor the dimensions of *Hyostragulum mobile* on *Thalesoceras amaltheum* differ from *Hyostragulum mobile* that resides on *Pterygotheca.*

The morphology of this single case of *Hyostragulum* growing on *Thalesoceras amaltheum* adds to the understanding of the morphology of *Hyostragulum* itself. While growing over the dorsal sides of hyolithids the *Hyostragulum* coralla are restricted by the size and morphology of the narrow shell, but growth on the cephalopod shell shows no such restrictions. Nevertheless, the *Hyostragulum* corallites are oriented along the cephalopod conch's axis not only by their median septa, but also by the elongation of the corallites. We consider this to be evidence for genetic constraint on the morphology of *Hyostragulum*, and not morphologic restriction placed on the animal by the dimensions of the usual hyolithid hosts. The shape and median septa alignment probably evolved by growing on hyolithids. Its growth on a cephalopod was possible because micro conditions for the larva to settle were met, but the basic astogeny (Boardman and Cheetham 1973) remained intact, thereby resulting in the same adult morphology as on a hyolithid. We consider this to be proof of co-evolution.

Bryozoans on hyolithids

Epibiotic bryozoans on hyolithids were described from the Ordovician of North America (Duncan 1957), and their co-occurrence is known (but unpublished) from Scandinavia and the Baltic states. Taylor and Wilson (2002) also cite the personal communication of Brett on the "specificity of encrustation of *Hyolithes* by prasoporid bryozoans... in the Ordovician Trenton Group of New York and Lexington Limestone of Kentucky". Epibiotic bryozoans are relatively abundant in a few localities that were tropical to near tropical in the Ordovician, but have not been found in Bohemia where the waters were cold during that time. Epibiotic bryozoans are also known to grow on living Silurian orthoconic cephalopods (Baird et al. 1989).

Zoaria of epibiotic bryozoans encrusting hyolithid conchs commonly cover an entire hyolithid conch, and in all observed cases their zooecia are conspicuously differentiated or polarized. Zooecia on the ventral (less inflated) side of the hyolithid shell are conspicuously shorter, have smaller diameters than those on the dorsal side, and are more variable. In contrast, zooecia of the dorsal side are normally developed, i.e. they do not differ from those growing on the sea bottom and/or on substrates other than hyolithids. The biomass of the upper dorsal surface is much greater than on the ventral (cryptic) surface of the conch.

We concur with Morris et al. (1991) that bryozoans, both fossil and recent, do not extend their bodies into the soft substrate and are not, in the strict sense, infaunal, except in sandy sediments (Spjeldnaes 2000).

Bryozoan epibionts and life position of Ordovician hyolithids

Hyolith-bryozoan symbiosis from the Kukruse Formation, Estonia

Undescribed hyolithid specimens occur in the Ordovician of Estonia (Kukruse Stage, represented by the Viivikonna Formation, a 3–20 m thick sequence of grey argillaceous calcarenitic limestones with intercalations of kukersite (oil shale) and kukersitic marls, lowest Upper Ordovician, approximately equivalent to the Blackriverian in North America). They are commonly covered over both their dorsal and ventral sides with the bryozoan determined as *Leptotrypa hexagonalis* Ulrich, 1890. The present authors are not convinced that the Estonian specimens are conspecific with those of North America. The hyolithid conchs are slender, with an apical angle of 15–20°. They have pronounced radial ribs combined with much finer growth lines outlining the ligula on their ventral side.

The basal parts of the bryozoan zooecia are directed toward the hyolithid aperture, but subsequently abruptly turn to face almost perpendicularly to the surface of the hyolithid conch (Plate II, fig. 1), and in some cases are angled toward the aperture at an angle less than 50°. The zooecia after deflection maintain their growth direction throughout their entire length and are mostly hexagonal in tangential section.

A single (typical) specimen was serial sectioned, and acetate peels were prepared. All the sections show the bryozoan zoarium differentiated into long, large-diameter, thick-walled, and scarcely diaphragmated zooecia that grew on the more inflated dorsal side of the hyolithid. Shorter, small-diameter, thin-walled, and densely diaphragmated zooecia grew on the less inflated ventral side of the hyolithid conch. In general, on specimens from various Ordovician localities, the morphology of bryozoans on hyolithids is much the same: 'normal' sized (the same as specimens growing on the sea bottom or on other substrates) zooecia on the dorsal surface, smaller ones on the ventral surface.

In Plate II, figs 2–4 the smaller ventral zooecia reach 4/5ths of the length of the larger dorsal ones; their diameter (measured only on the longitudinal section) is about half that of the larger dorsal ones, as is the thickness of the respective zooecial walls. While large dorsal zooecia may occasionally contain one or two diaphragms, they are commonly missing; small ventral zooecia have three to eight well developed, slightly concave, and usually complete diaphragms.

Bryozoan zooecia on the ventral side of the conch grew over the sidewalls of the zooecia of the dorsal side (Plate II, figs 2–4). This strongly indicates that in this case the ventral zooecia grew later and at a slower rate than the dorsal ones.

Hyolith-bryozoan symbiosis from Wisconsin, U.S.A.

The specimens of an undescribed hyolithid covered with the bryozoan *Leptotrypa hexagonalis* and *Mesotrypa ex-*

pressa were described by Duncan (1957) from the Ordovician, Black River (Caradocian), at Mineral Point, Wisconsin. The type specimens of both *L. hexagonalis* and *M. expressa* were described from this locality. We know the hyolithids only from acetate peels. The bryozoans usually cover both dorsal and ventral sides of the hyolithid shell. The thickness of the bryozoan colony on the dorsal side is much greater than on the ventral side (up to five or six times thicker). Bryozoan zooecia on the dorsal side of the hyolithid conch, like those seen in the Kukruse, are slightly larger in diameter than on the ventral side. Diaphragm density within dorsal and ventral zooecia is, however, very similar. Zooecia of both dorsal and ventral sides begin their growth almost recumbently on the hyolithid conch with their apertures directed towards the hyolithid aperture. The zooecia early in astogeny abruptly elevate above their substrate and gradually change direction to become almost perpendicular to the conch surface (Plate II, figs 7 and 8).

One of the Wisconsin specimens has been serial sectioned. Acetate peels of the serial sections are figured on Plates III and IV, figs 1–16. Serial sections show the usual differentiation of bryozoan zooecia on dorsal and ventral sides of the hyolithid shell. It is clear that the smaller zooecia of the ventral side grew over the walls of larger dorsal zooecia; it further confirms our observation that zooecia on the ventral side grew later than those on the dorsal side. The bryozoan on the apical part of the sectioned shell is notable (Plate IV, figs 9–16): differentiation of the zooecia disappears, the direction of their growth becomes chaotic, and eventually (Plate IV, figs 15 and 16) the length and diameter of both dorsal and ventral zooecia becomes equal. In our opinion this strongly indicates that the apex of the hyolithid conch was elevated above the substrate.

Discussion

Classification of symbiosis

The Devonian tabulate coral *Hyostragulum* is an obligate symbiont of hyolithids. It has never been found on other hosts (with the single exception of a cephalopod) or on any other substrate. Conversely, hyolithids are not the obligate symbionts of *Hyostragulum.* Most hyolithids do not host any epibionts, while individuals of the species known to bear *Hyostragulum* occur with and without epibionts together in the same population. This observation is supported by extensive data from the St. Prokop locality.

Bryozoans (our observations are limited to the Ordovician) are different in several aspects: they are neither the obligate symbionts of hyolithids, nor are the hyolithids obligate symbionts of bryozoans.

According to the classification of Darrell and Taylor (1993) of fossil macrosymbioses, both Devonian and Ordovician symbioses described above are encrustations. In accord with their definition of concurrent growth, they are also tabulate and bryozoan symbionts that started their growth in the young apical part of the hyolith conch and grew toward the aperture, but never grew over the hyolithids' operculum.

Another classification of symbioses is that of Lewis (1985) who recognized a number of distinct interactive categories, some of which are important for our discussion. They noted: a) duration of association (in our examples it is permanent), b) physical contact between symbionts (they are ectosymbiotic), c) taxonomic specificity (in our cases they are specific), d) nutritional relationships of associates (tabulates and bryozoans probably gain by being oriented into the current), e) interdependence of symbionts (obligatory for *Hyostragulum,* facultative for both Devonian and Ordovician hyoliths and for bryozoans), and f) integration between partners. Both *Hyostragulum* and symbiotic bryozoans developed morphologies different from this in non-symbiotic specimens. In *Hyostragulum* the morphological changes are irreversible – see *Hyostragulum* on the cephalopod *Thalesoceras amaltheum* (Plate I, fig. 12). In bryozoans the changes are reversible as described above. Hyolithids did not visibly develop a special morphology. Lewis's (1985) classification according to mutual gains and losses (g) shows that the smaller symbiont, either *Hyostragulum* or bryozoans, in addition to acquiring a hard substratum, gained the potential to be moved into the current, while the host (the hyolithid) probably gained a defensive covering and increased stability. We thus classify the associations described above as at least neutralism but more probably mutualism.

Darrell and Taylor (1993) state that "equivocal evidence of life association may be derived from the orientation and location of associates". In our case, the life position of hyoliths was derived from their epibionts' orientation (Marek and Galle 1976).

Darrell and Taylor (1993) noted to their surprise the rarity of obligate and species-specific symbioses in the fossil record. They listed the *Hyostragulum-Pterygotheca* symbiosis (Table 1; p. 189) but did not discuss it further. We argue that the symbiosis of *Hyostragulum* and hyolithids is obligatory, as *Hyostragulum* occurs on no other substrate (with the single exception of *H. mobile* on a cephalopod). The symbiosis of *Hyostragulum mobile* can also be species-specific as in the case of the Lower Devonian St. Prokop Quarry, where the tabulate *H. mobile* occurs exclusively on a single host, the hyolithid *Pterygotheca barrandei.* While the smaller obligate symbiont, *H. mobile,* shows adaptations for a life in symbiosis (elongation of corallites along host hyolith's axis, see Plate I, fig. 3), the larger hyolithid host shows no such adaptations: it is non-obligate, and is known to live independently of such an association (this is also in accord with Darrell and Taylor 1993).

Although it is almost impossible to prove co-evolution where evolutionary change in one of symbionts is followed by change in the other (Futuyma and Slatkin 1983), we suggest that such a process can be suspected for both Devonian and Ordovician encrusting symbionts described above. Our reasons are as follows: 1) That the *Hyostragulum* corallites are oriented along the cephalopod conch's axis in the same manner as on hyolithid conchs. We consider this to be evidence for genetic constraint on the morphology of *Hyostragulum.* The shape and median septa alignment probably evolved by growing on hyolithids. Its growth on a cephalopod followed the basic astogeny, and thereby resulted in the same adult morphology as present on a hyolithid. And 2) perhaps the chemical composition of the juvenile periostracum allowed the epibiont to settle, or it may indeed attract the juvenile epibiont to settle. It should be noted that hyolithids are the preferred hosts of epibionts, and that this feature might have evolved in mutualistic relation to epibionts (bryozoans in the Ordovician, and tabulates in the Devonian).

Site selection

Current orienting hyolithids are desirable resting sites for certain species of tabulate corals and trepostome bryozoans, and rarely for other (unrecognisable) organisms. Because epibionts settle on the oldest (juvenile) portion of the hyolithid, it suggests to us that site selection is quite important, and perhaps the chemical composition of the juvenile periostracum allows the epibiont to settle. This feature might have evolved in mutualistic relation to epibionts. Such early recruitment secured the entire available substrate for a single coral or bryozoan colony, and is in keeping with observations by Grosberg (1981) that small substrates are more likely to be completely covered by a single species. No multiple recruitments or competition for space by two or more species were observed in this study. This appears to be due to a mutualistic relationship and possibly also to co-evolution. The hyolithid keeps the epibiont in an optimum position, faced into the current for food, oxygen, and waste removal. The colony on the dorsum of the conch provides added protection and additional mass for stability. This can be especially important in higher current regimes (hence more food, oxygen, and easier waste removal), or where the animal lives in habitats subject to destabilizing currents.

There are numerous benthic invertebrates that could provide a potential settling surface for epibionts. Curved faces on the upper parts of clams, gastropods, and brachiopods can provide hydrodynamic surfaces that locally increase current velocity as described by Bernoulli's Principle and, like hyolithids, should make acceptable resting spots for larvae to attach to and grow. In our opinion, the fact that this does not occur is probably due to the defence mechanisms of the potential hosts, which indicate that for their specific life-modes it is better to defend against habitation. The periostracum is known (Taylor and Wilson 2002) to be the first line of defence in many shelled molluscs, and it probably contains toxins that retard the growth of epibionts (Bottjer 1981, Thompson 1985). Recruitment patterns depend on the physical and chemical composition of the substrate (Roberts et al. 1991), the presence or absence of other macro- or micro-epibionts (Brancato and Woollacott 1982, Kitamura and Hirayama 1987, Wieczorek and Todd 1998, Hamer and Walker 2001), their colours (Pomerat and Reiner 1942), and on the anti-fouling activities of potential substrate organisms (Wahl 1989, Uriz et al. 1991). The fact that hyolithids are virtually the only invertebrates in some populations to have any type of (preserved) epibionts clearly indicates that they are either defenceless against them or that they deliberately provide a welcoming substrate (see Wahl 1989).

The growth of epibionts

Judging from the uniform orientation of the zooecia on all observed infested hyolithid shells, it is clear that both tabulates and bryozoans grew over the dorsal and upper lateral surfaces of the living hyolithid conch. As stated above, our observations show that hyolithid/coral and hyolithid/bryozoan colonies assume a very similar morphology.

Pomerat and Reiner (1942) found that bryozoans prefer undersides on experimentally submerged glass surfaces. Bryozoan zooecia growing on the ventral side of the hyolithid conch are smaller than those of the dorsal side. We can therefore assume one of two possible modes of growth: 1) that the dorsal and ventral parts of the epibiont grew at separate times (and also at different rates), or 2) they grew simultaneously. In both cases, but especially in the latter case, it is suggested that the ventral sides of the hyolithid hosts were in, or helped create, a distinct restricted type of cryptic environment for the epibionts, which is indicated by the bryozoan's downward growth direction and especially by its small size (Wood 1999, p. 211, tab. 6.2). A restricted, ventral side environment could have been created if the hyolithids used their helens as support to elevate the anterior end of the conch. However, there is no fossil evidence to support this conjecture. Cryptic space on the hyolithid ventral side provided a well-protected microenvironment (Gischler and Ginsburg 1996). The crypt-living part of the bryozoan colony suffered mainly by resting directly or nearly on the sediment.

If zooecia grew simultaneously on both the top and bottom of the hyolithid conch it is likely to have occurred close to the aperture. Because conchs are commonly slightly convex along the ventral surface, the lip is raised slightly above the substrate. Also, downward stabilizing movements by the helens would also tend to slightly elevate the anterior end. Such modifying factors may well produce the cryptic conditions that could result in bryozoans encrusting on the anterior underside of the conch. Towards the conch's posterior end the bryozoans may have died.

We can only speculate why Devonian age *Hyostragulum* did not grow over the ventral surface of hyolithids. Epibiont tabulates may have had zooxanthellae, and photosynthesis would not have been possible. Also, the food gathering mechanism of the tentacles may have functioned poorly in this cryptic environment.

Life position of hyolithids

In Plate IV, figs 14 and 16 the length of both dorsal and ventral zooecia is equal. In our opinion this strongly indicates that the apex of the hyolithid conch was elevated above the substrate. Anterior parts of the hyolithid conch are covered with differentiated zooecia. We interpret this to mean that the apex of the conch did not touch the sea bottom, while most of the ventral part of the conch was in light or varying contact with the bottom (providing the crypt environment).

In soft sediments hyolithids like the Devonian *Pterygotheca* and *Ottomarites,* as well as other undescribed Devonian *Hyostragulum*-bearing hyolithids, could have rested on the entire length of the conch on the sea bottom.

Conclusions

1. In the cases observed in this study the epibionts prefer hyolithids to any other host in the Ordovician and in Devonian. In our opinion, either the juvenile periostracum of hyolithids allowed the epibionts to settle, or its composition attracted the epibionts. This feature of hyolithid periostracum might have evolved in a mutualistic relation to the epibionts, and is one of our reasons for proposing mutualism and co-evolution.
2. The morphology of epibiotic *Hyostragulum* growing on cephalopods does not differ from that on the restricted space of hyolithid dorsum. We consider this as evidence for genetic constraint on the morphology of *Hyostragulum.* This is another of our reasons for proposing mutualism and co-evolution.
3. The Devonian tabulate coral *Hyostragulum* is an obligate symbiont of hyolithids, and its morphological changes are irreversible. However, hyolithids are not the obligate symbionts of *Hyostragulum.*
4. The Ordovician bryozoans and hyolithids discussed herein are only facultative symbionts.
5. The described symbiotic relations of hyolithids and their epibionts suggest co-evolution, though it cannot be unequivocally proven.

Acknowledgements. The authors are indebted to following persons listed in alphabetic order, without whose help the research reported in this paper would have not have been possible: the late Dr. V. Havlíček, emeritus member of the Czech Geological Survey, Prague, for consultations on and determination of brachiopod taxa; Dr. R. Horný, National Museum (Natural History), Prague, for the determination of gastropods and for making available the National Museum's collection of gastropods from St. Prokop Quarry; Dr. J. Kříž, Czech Geological Survey, Prague, for the determination of pelecypods and consultations on their ecology; Dr. Š. Manda, Czech Geological Survey, Prague, for advice on cephalopods; Prof. J. Marek, Charles University, Prague, for making available the collection of Ing. F. Hanuš, deposited in the Faculty of Natural History, Charles University, Prague; and Dr. J. Vaněk, Prague, for determination and consultation on trilobites. We also thank the reviewers, Messrs. Prof. Andreas May, Saint Louis University, Madrid Campus, Spain, and Mgr. Martin Valent, Charles University, Institute of Geology and Paleontology, Prague, Czech Republic, and one anonymous reviewer whose constructive comments led us to more precise and clear formulations and opinions. The present paper originated as a result of Grant A 3013807 'Hyolith-Epibiont Relationships: Taxonomy, Nature of Symbiosis, and Spatial/Temporal Distribution', and a current grant IAA3013207 'Devonian coral fauna of the Bohemian Massif', both projects funded by the Grant Agency of the Czech Academy of Sciences. It is part of the Czech Academy of Sciences Research program CEZ Z3 013 912.

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Plate I

All the specimens figured are stored in the Department of Paleontology, National Museum, Václavské náměstí 168, CZ-115 79 Praha 1, Czech Republic. Photographs were made by Hana Vršťalová, Czech Geological Survey, except fig. 3, which was made by Josef Brožek, Geological Institute of the Academy of Sciences of the Czech Republic, and fig. 4 was made by Dana Hejdová, Czech Geological Survey. All specimens were coated with ammonium chloride before photographing, except the specimens in figs 3 and 4.

1–3 – *Hyostragulum mobile* Marek and Galle, 1976, holotype, specimen GLÚ LM 130, Praha-Hlubočepy, St. Prokop Quarry, Dvorce-Prokop Limestone, Pragian, Lower Devonian, on the negative of the conch *Pterygotheca barrandei* Novák, 1891. 1 – dorsal view of the apical part of the corallum, × 5.1. 2 – lateral view of the same corallum, × 5.1. 3 – ventral view with elongated corallite bases and median septa visible (× 6.2).

4 – *Hyostragulum mobile* Marek and Galle, 1976, paratype, specimen LM 158, Praha-Hlubočepy, St. Prokop Quarry, Dvorce-Prokop Limestone, Pragian, Lower Devonian, longitudinal section through two corallites with visible tabulae, × 18.5.

5–8 – *Hyostragulum mobile* Marek and Galle, 1976, paratypes, Praha-Hlubočepy, St. Prokop Quarry, Dvorce-Prokop Limestone, Pragian, Lower Devonian, on the conchs of *Pterygotheca barrandei* Novák, 1891. 5 – specimen LM 131, dorsal view, × 3. 6 – the same specimen, lateral view, × 3. 7 – the same specimen, ventral view, × 3. 8 – specimen LM 139, dorsal view; corallum removed, remains of weathered $CaCO_3$ skeleton indicate positions of the corallites and median septa, × 2.5.

9, 10 – *Hyostragulum annae* Galle and Plusquellec, 2002, holotype, specimen NM L 13957, Koněprusy, Suchomasty Limestone, Zlíchovian-Dalejan, Lower Devonian, on the conchs of *Ottomarites discors* (Barrande, 1867). 9 – polished transversal section with short corallites on the dorsal side of the conch, × 5. 10 – the same specimen, ventral view with narrow holothecal fringe, × 2.5.

11 – *Hyostragulum annae* Galle and Plusquellec, 2002, specimen GLÚ LM 133, wide holothecal fringe on the conch's ventral surface of ?*Pterygotheca barrandei* Novák, 1891, × 3.3.

12 – *Hyostragulum mobile* Marek and Galle, 1976, specimen GLÚ LM 161, Praha-Hlubočepy, St. Prokop Quarry, Dvorce-Prokop Limestone, Pragian, Lower Devonian, on the conch of *Thalesoceras amaltheum* Manda, 2001, × 5.

Plate I

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Plate II
Illustrated acetate peels were photographed through the microscope in either lightfield or darkfield lighting. Specimens illustrated in figures 1–4 are from Ordovician of Kukruse, Estonia. Material (acetate peels) is housed in the National Museum of Natural History, Smithsonian Institution, Washington D. C., USA.
1 – specimen PA 30041, dorsal view of slender hyolithid conch with radial ribs and fine growth lines, covered with the bryozoan ‘*Leptotrypa hexagonalis*’. Its zooecia are arranged toward the aperture but subsequently abruptly turn to face almost perpendicularly the axis of the hyolithid conch, × 5.5.
2–4 – specimens PA 030034, PA 030035 and PA 030032, acetate peels. Transverse sections through hyolith conch with smaller ventral and larger dorsal zooecia. Diaphragms in the dorsal zooecia are commonly missing; ventral zooecia have well-developed diaphragms. Bryozoan zooecia of the ventral side of the conch grew over the sidewalls of the zooecia of the dorsal side. This strongly indicates that the ventral zooecia grew later than the dorsal ones, × 5.
5–8 – specimens of the Ordovician age [Black River (Platteville)], from Mineral Point, Wisconsin, U.S.A. Material is housed in the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA, and are identified as USNM 44057 and USNM 57284. Duplicate acetate peels figured in figures 5–8 are stored in the National Museum (Natural History), Prague, Czech Republic. 5 – specimen S 4723, acetate peel, transverse section, lightfield. This specimen is the holotype of *Leptotrypa hexagonalis*, numbered USNM 44057. The bryozoan zoarium on the ventral side of the shell is preserved only on the lower side of the dorsal part of the colony, × 5.5. 6 – specimen S 4724, acetate peel, transverse section, lightfield. This specimen is the paratype of *L. hexagonalis*, numbered USNM 44057. Its colony is arranged in the same manner as in previous illustration. The hyolithid conch is deformed, probably by pressure from overlying sediment, × 5.5. 7, 8 – specimen S 4725, acetate peel, longitudinal section. This specimen is the holotype of *Mesotrypa hexagonalis,* numbered USNM 57284. The hyolithid conch has long and wide bryozoan zooecia on its dorsal and short narrow ones on ventral side. Note the large dorsoventral apical angle. 7 – lightfield, 8 – darkfield, × 5.5.


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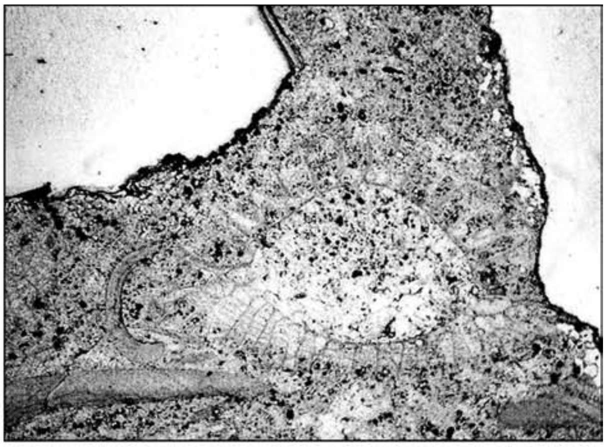
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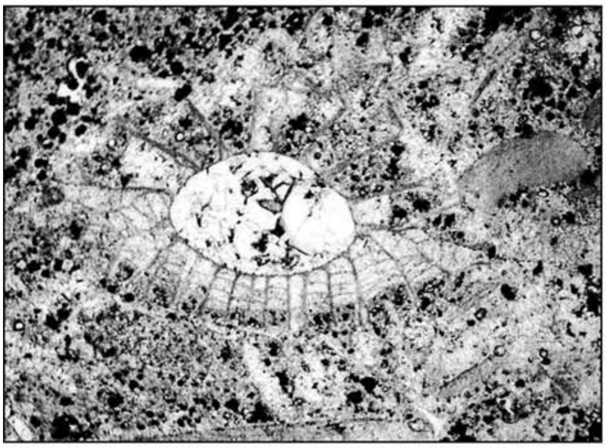
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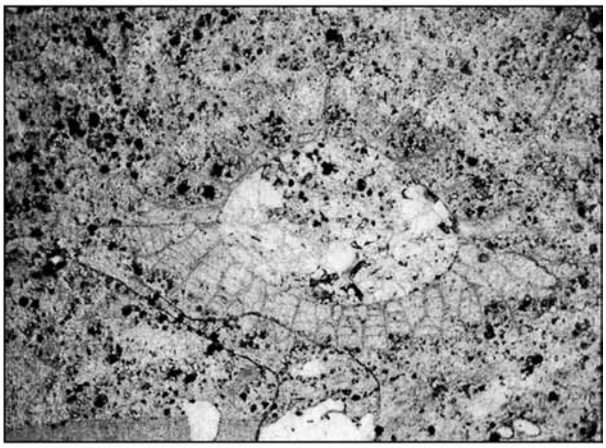
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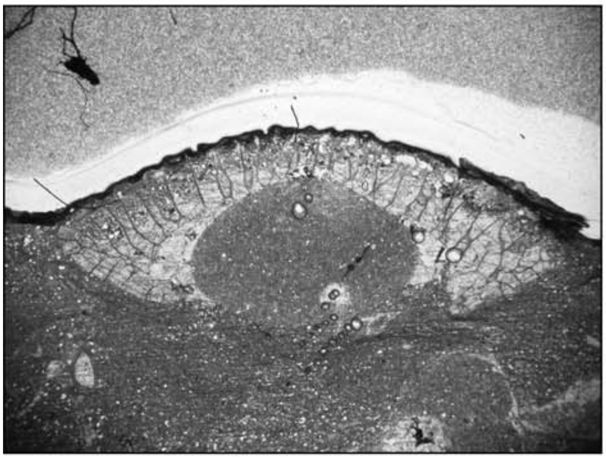
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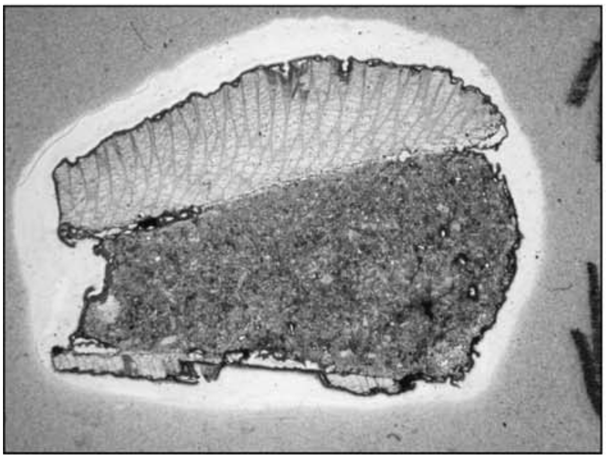
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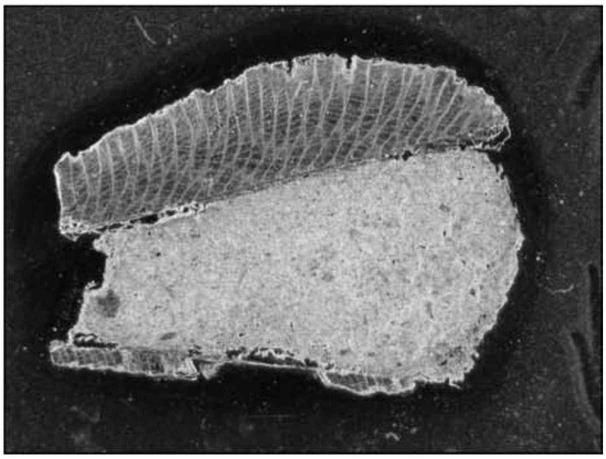
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Plate II

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Plate III
1–8 – serial sections of a single specimen. The specimen has been destroyed by sectioning. Ordovician [Black River (Platteville)], from Mineral Point, Wisconsin, U.S.A. Material is housed in the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA, and are identified as USNM 44057. Duplicate acetate peels figured here on figures 1–8 are stored in the National Museum (Natural History), Prague, Czech Republic.
1 – peel S 4726, beginning of sectioning, length of specimen (LS) 25.3 mm, lightfield. Only small bryozoan zooecia are preserved on ventral side of hyolith shell, × 7.
2 – peel S 4727, LS 22.4 mm (2.9 mm ground off), lightfield. Bryozoan zooecia of the ventral side of the conch grew onto the sidewalls of the zooecia of the dorsal side, as the ventral zooecia apparently grew later than the dorsal ones, × 7.
3 – peel S 4728, LS 21.4 mm (1.0 mm ground off), lightfield. Large zooecia on the dorsal side of the conch without diaphragms, small zooecia on the ventral side of the conch grew over them, × 7.
4 – peel S 4729, LS 20.5 mm (0.9 mm ground off), lightfield. The same arrangement of zooecia, diaphragms appear also in large zooecia of the dorsal side of the conch, × 7.
5 – peel S 4730, LS 20.2 mm (0.3 mm ground off), lightfield. The same arrangement of zooecia, they are still differentiated, × 7.
6 – peel S 4731, LS 19.3 mm (0.9 mm ground off), lightfield. The same arrangement of zooecia, they are still differentiated, × 7.
7 – peel S 4732, LS 18.6 mm (0.7 mm ground off), lightfield. The same arrangement of zooecia, they are clearly differentiated, × 7.
8 – peel S 4733, LS 18.1 mm (0.5 mm ground off), lightfield. Zooecia are differentiated but those on the dorsal side of the conch are almost of the same length as the ventral ones, × 7.

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Plate IV
9 – peel S 4734, LS 17.1 mm (1.0 mm ground off), lightfield. Zooecia are essentially undifferentiated, their arrangement is somewhat chaotic, × 7.
10 – the same peel in darkfield, × 7.
11 – peel S 4735, LS 16.9 mm (0.2 mm ground off), lightfield. Zooecia undifferentiated, their arrangement is somewhat chaotic, × 7.
12 – the same peel in darkfield, × 7.
13 – peel S 4736, LS 16.6 mm (0.3 mm ground off), lightfield. Zooecia are undifferentiated, their arrangement is chaotic, × 7.
14 – the same peel in darkfield, × 7.
15 – peel S 4737, LS 16.3 mm (0.3 mm ground off), darkfield. End of the sectioned specimen. Zooecia are undifferentiated, their arrangement is strongly chaotic. The end of the hyolith conch was probably elevated above the substrate, × 18.
16 – the same peel in darkfield, × 18.


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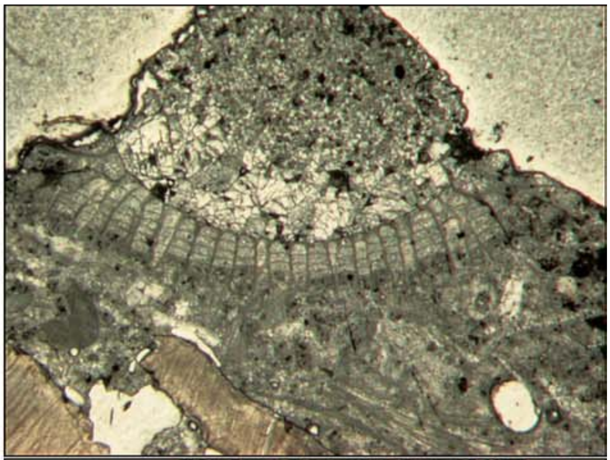
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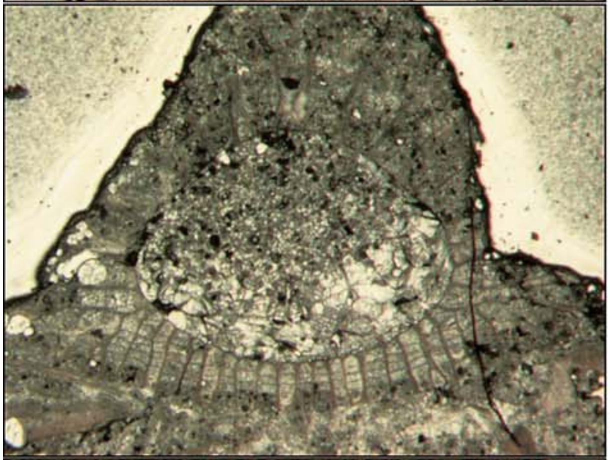
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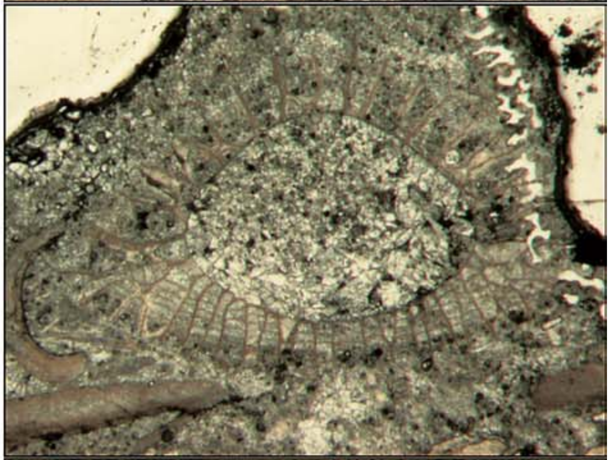
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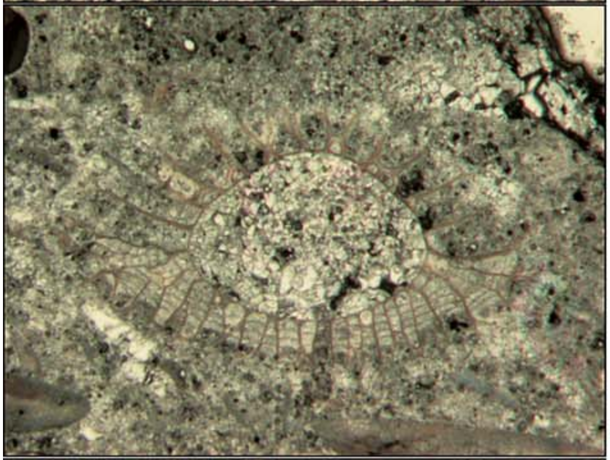
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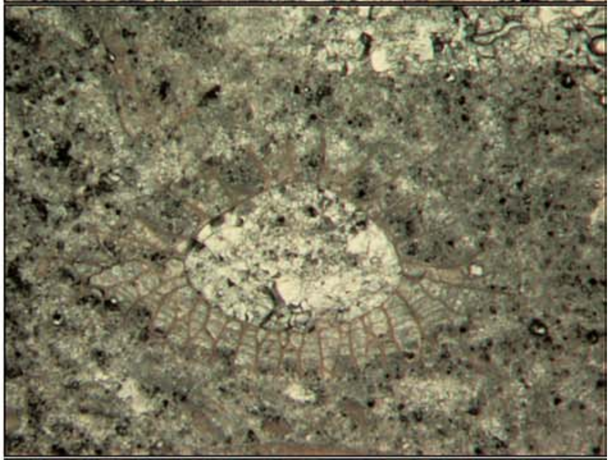
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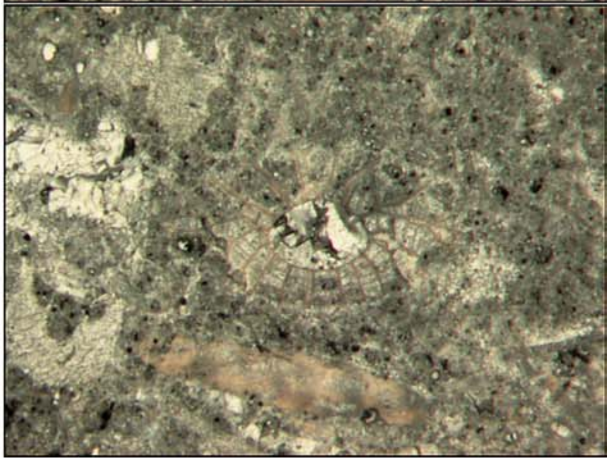
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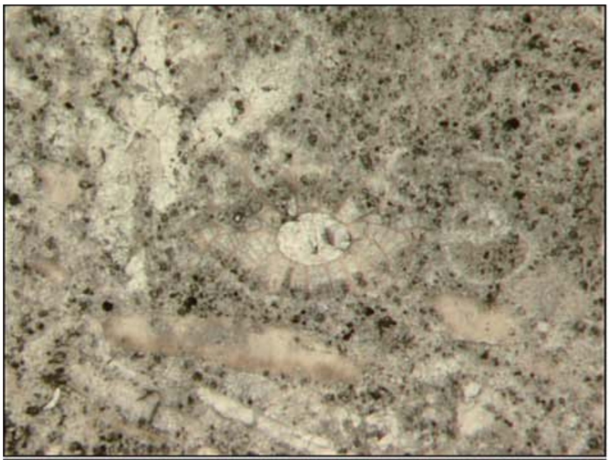
Plate III



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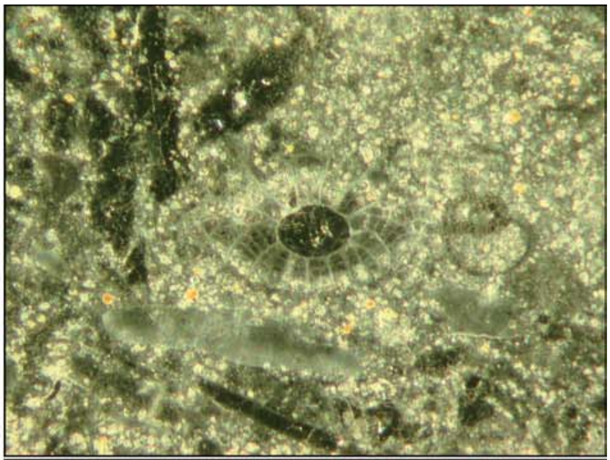

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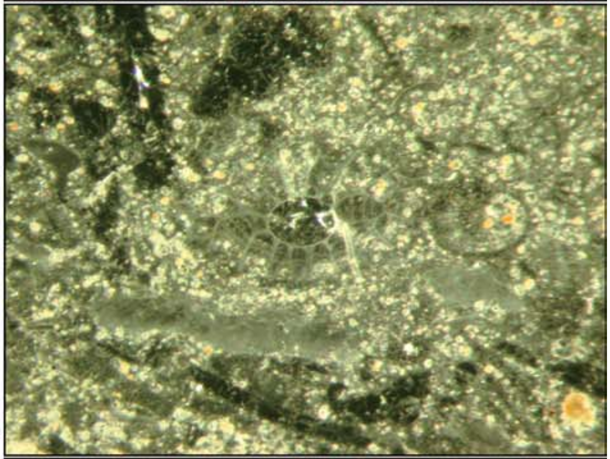

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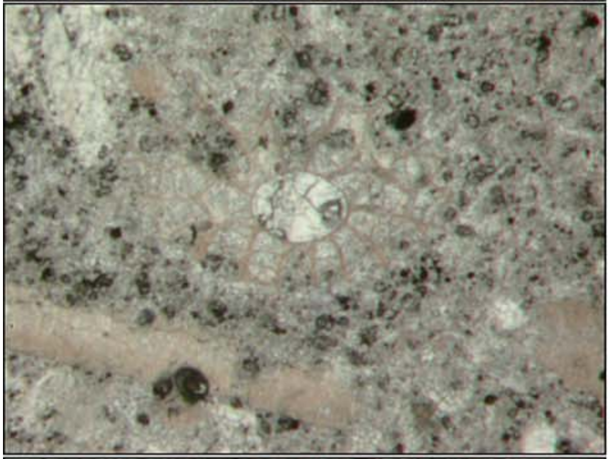

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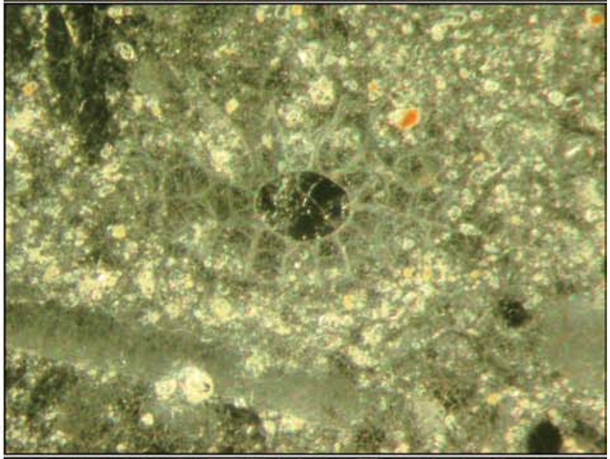

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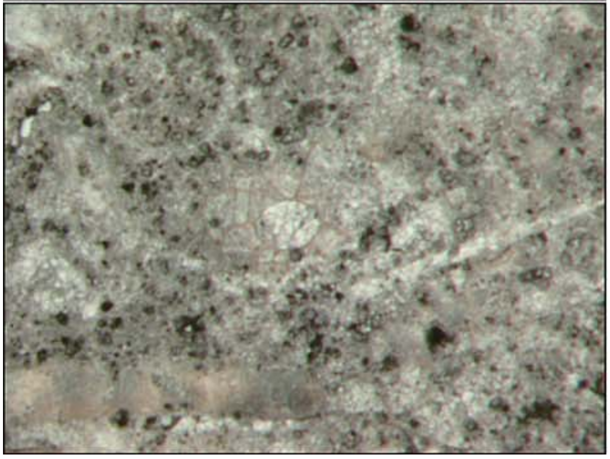

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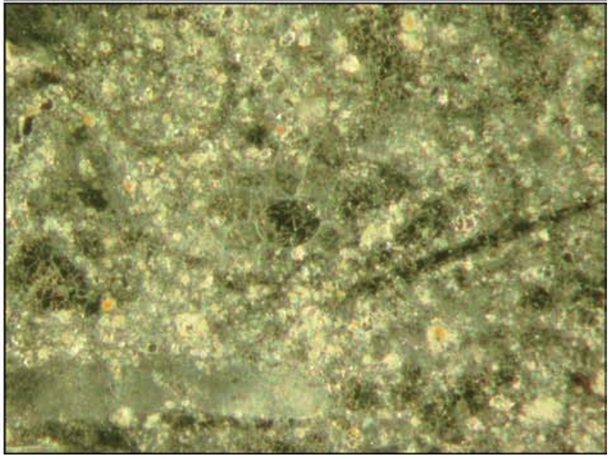

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Plate IV